SHORT COMMUNICATION

Control of plant growth by nitrogen: differences between cereals and broadleaf species

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Abstract. In four dicotyledonous species low levels of N strongly inhibited leaf expansion during the day but had little or no effect at night. In contrast, daytime and night-time expansion were equally affected in four cereal species. The results support the general concept that in dicotyledons, N controls leaf expansion through its effects on hydraulic conductivity. In such N-limited plants, water deficits generated by transpiration may inhibit daytime cell expansion. In cereals, cell expansion and transpiration occur in separate zones of the leaf and are apparently unrelated.

Growth analysis showed that low levels of N inhibited leaf area growth more strongly in dicotyledons than in cereals, but had similar effects on net assimilation rates of plants in the two groups. As a result, dry matter production was more efficient in cereals than in dicotyledons when N was limiting.

Nitrogen fertility strongly affects plant growth and productivity. Two generally recognized reasons are that N alters (1) leaf area and (2) net photosynthetic rate (Novoa & Loomis, 1981). After many years of study, though, the relationship of these characters to each other and to productivity remains confusing and controversial. Some workers have suggested that growth limitation by low N results mainly from decreased photosynthetic rate, whilst other effects are secondary (Natr, 1975; Bolton & Brown, 1980). Others have shown that low N specifically inhibits leaf area growth, with photosynthetic rate affected only at more severe N stress (Watson, 1952; Bouma, 1970; Motta & Medina, 1978). This latter view gains support from the accumulation of carbohydrates in N-limited plants (Radin, Parker & Sell, 1978) and also from the observation that low N limits leaf size by restricting cell expansion, not cell division (Morton & Watson, 1948; Radin & Parker, 1979).

Recently Radin & Boyer (1982) found that low N strongly decreased the hydraulic conductivity of sunflower plants, thereby increasing water deficit in the expanding leaf blades. In turn, turgor was decreased in the expanding leaf cells and turgor-dependent growth was inhibited. The water deficit which slowed leaf expansion in N-limited plants was generated by transpiration; and expansion was restricted mostly during the daytime when transpiration was most rapid (Radin & Boyer, 1982).

Sunflower is typical of dicotyledonous (broadleaf) plants in that cell expansion occurs in leaf blades which are exposed to the air, and therefore transpiring. Subjection of the expanding cells to diurnal water deficits is thus unavoidable. In members of the Gramineae (grass family), cell expansion occurs at the base of the leaf blade. This zone is protected from the atmosphere by the sheath of the preceding leaf, and thus there is little transpiration from the zone of elongation. It can be inferred that the effects of N on leaf enlargement in grasses might differ from those in broadleaf plants. It is suggestive that with some exceptions (e.g. Gregory, 1926; Medina, 1970; Wilson, 1975), evidence favouring a specific effect of N on leaf area has been more striking and clear-cut when obtained from broadleaf plants than when obtained from cereals. Here I report experiments which clearly differentiate between growth of cereals and of broadleaf plants when N is limiting.

Plants were grown in a greenhouse with daily maximum and minimum temperatures of approximately 30 and 21°C, respectively. The dewpoint of the air varied between 10 and 15°C (a relative humidity of 30–40% during the afternoon). Plants were watered with nutrient solutions containing either high or low N concentrations. Diurnal leaf enlargement patterns of four cereals (wheat, barley, corn, and sorghum) were compared to those of four broadleaf species (sunflower, cotton, soybean, and radish). In cereals, growth inhibition by low N was similar during the day and the night (Table 1). In broadleaf plants, though, growth inhibition was clearly more severe during the day than at night. Although corn and sorghum are C_4 plants, the photosynthetic pathway seemed unrelated to any effects of N, because the other two cereals are both C_3 plants (but see Wilson, 1975).

Table 1. Effect of low nitrogen availability on leaf growth of cereals and broadleaf plants.

Species	Growth inhibition by low N (%)	
	Daytime	Night-time
Cereals		
Wheat (*Triticum aestivum* L., cv. Produra)	19 ± 3	14 ± 4
Barley (*Hordeum vulgare* L., cv. Numar)	15 ± 9	20 ± 2
Sweet Corn (*Zea mays* L., cv. Golden Cross)	12 ± 5	11 ± 6
Sorghum (*Sorghum bicolor* Moench., cv. NK 222G)	18 ± 2	27 ± 6
Broadleaf plants		
Sunflower (*Helianthus annuus* L., cv. Russian Mammoth)	55 ± 8	23 ± 7
Cotton (*Gossypium hirsutum* L., cv. Deltapine 70)	56 ± 7	10 ± 2
Soybean (*Glycine max* Merr., cv. Wayne)	56 ± 9	-9 ± 7
Radish (*Raphanus sativus* L., cv. Comet)	46 ± 8	7 ± 2

Plants were grown in pots containing sand and watered with a complete nutrient solution containing either $0.5 \, \mathrm{mol \, m^{-3}}$ (low N) or $5 \, \mathrm{mol \, m^{-3}}$ (high N) NO_3^- as K^+ and Ca^{2+} salts (except that the high N solution for soybeans contained $15 \, \mathrm{mol \, m^{-3}} \, NO_3^-$). Low N solutions contained $4.5 \, \mathrm{mol \, m^{-3}} \, Cl^-$ as a substitute for the NO_3^-. Leaf growth rates were followed by measuring blade lengths of the third leaf in cereals and soybean, the second leaf in sunflower and radish, and fourth leaf in cotton. Measurements were made approximately at sunrise and sunset to separate daytime and night-time mean growth rates. All data are means of 8 to 12 plants, and are shown $\pm$ standard error.

Figure 1 shows the growth rates of cotton and barley leaves throughout their development. These results are typical of all the species surveyed in each group. In barley, the daytime expansion rate was consistently greater than the night-time rate, regardless of N nutrition or leaf age, until leaves approached their maximum lengths. This pattern has previously been ascribed to diurnal temperature fluctuations (Acevedo *et al.*, 1979; Cutler *et al.*, 1980; Kemp & Blacklow, 1980). In cotton, though, the rate of leaf expansion shifted from a daytime maximum early in leaf development to a night-time maximum as the leaf became more nearly mature. This occurred because the daytime rate ultimately declined to almost zero while the night-time rate remained more or less constant. The point at which 'cross-over' of daytime and night-time rates occurred depended strongly upon N nutrition, with low N promoting an early shift to the night-time maximum (Fig. 1). Boyer (1968) established that in high N sunflower plants, the late decline in daytime expansion rate was from low hydraulic conductivity. The low N plants seemed to follow a similar pattern, except that hydraulic conductivity became limiting to expansion much earlier in leaf development. This argument is supported by the earlier demonstrations that hydraulic conductivity limits expansion of young low N leaves in sunflower (Radin & Boyer, 1982), and that low N decreases hydraulic conductivity in both sunflower and cotton (Radin & Parker, 1979; Radin & Boyer, 1982).

The difference between species in diurnal growth pattern (Fig. 1) was not from greater water stress in the cotton. Its midday leaf water potentials were in fact slightly higher than those of barley (data not shown). Instead, the spatial separation of
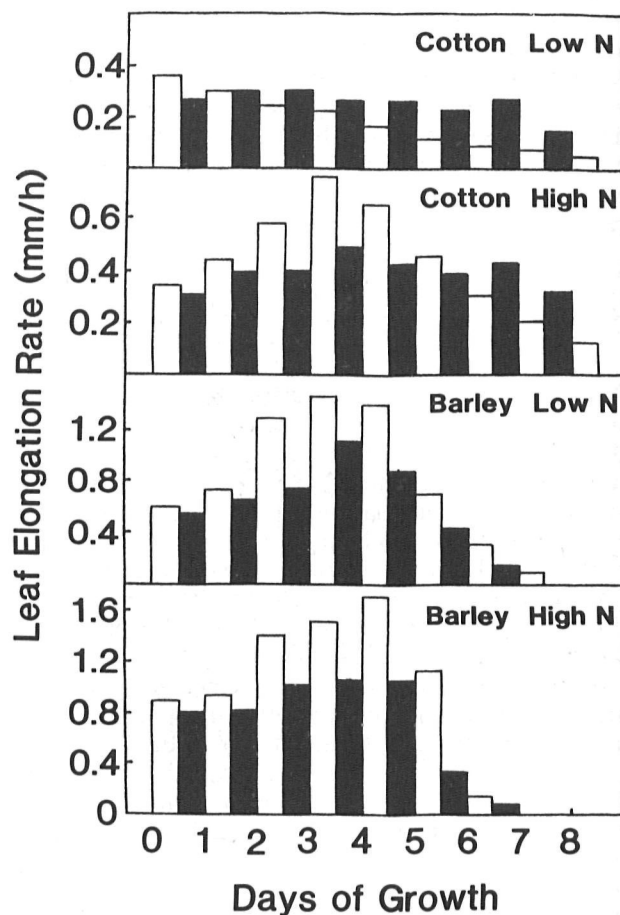

Figure 1. Enlargement rates of leaves of cotton and barley plants grown at two levels of N nutrition. Procedures were as described in Table 1. Measurements of leaf length were made along the midrib, beginning when length was about 2 cm. Open and dark bars indicate daytime and night-time rates, respectively.

transpiration and cell expansion in barley may have precluded the equilibration of water potentials in the two zones, and thus allowed turgor to be maintained in expanding cells at the base of the leaf despite water deficits in the blade. Such a disequilibrium requires only that there be a low conductivity for water movement between the expanding cells at the leaf base and the transpiring blade. This low conductivity for water movement into expanding cells has been well documented (Molz & Boyer, 1978; Matsuda & Riazi, 1981; Michelena & Boyer, 1982). Thus the rapid daytime expansion probably resulted mostly from the separation of the zone of elongation from the site of transpiration.

The restriction on leaf enlargement imposed by turgor in broadleaf N-limited plants is additional to any effects mediated directly by metabolism. Broadleaf plants might therefore be expected to show more severe long-term growth responses to low N than cereals (in which N nutrition has no apparent effect on daytime turgor). Growth analysis (Evans, 1972) of cotton and barley plants at two levels of N nutrition confirmed this suggestion. In cotton, when the relative accumulation of N was decreased 74% by N deficiency, the net assimilation rate ($g\,m^{-2}\,d^{-1}$) and the relative rate of leaf area increase ($m^2\,m^{-2}\,d^{-1}$) were decreased 31% and 56%, respectively (Table 2). The overall relative growth rate ($g\,g^{-1}\,d^{-1}$), which reflected both assimilation rate and partitioning into leaf area, was intermediate at 39% inhibition. In barley, a similar degree of N deficiency caused 26% and 25% decreases in the net assimilation rate and relative rate of leaf area increase, respectively. The overall relative growth rate was inhibited 25% (Table 2). Thus N deficiency of equal severity for these two species caused considerably greater growth reductions in the broadleaf plant than the cereal.

These results show that growth of broadleaf plants is more responsive to N than is that of cereals. The major reason for the difference is that in broadleaf plants, leaf area is affected to a greater degree than

assimilation. Clearly, hydraulic conductivity plays an important role in the broadleaf growth responses to N, and a lesser role in the cereal growth responses. In cereals, leaf expansion is apparently more closely linked to assimilation rate.

One clear implication of these findings is that cereals may use N more efficiently (relative to broadleaf plants) for dry matter production, especially when N is growth-limiting. However, the complexity of N effects on earliness, tillering or branching, etc., precludes the prediction of relative economic yields. The full ecological and agronomic implications of these findings have not yet been explored.

Acknowledgments

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Table 2. Nitrogen accumulation, growth, and assimilation rates of cotton and barley plants grown at two levels of N nutrition

Species and treatment	Relative accumulation rate (nitrogen) ($g\,g^{-1}\,d^{-1}$)	Relative growth rate (leaf area) ($m^2\,m^{-2}\,d^{-1}$)	Net assimilation rate ($g\,m^{-2}\,d^{-1}$)	Relative growth rate (dry mass) ($g\,g^{-1}\,d^{-1}$)
Cotton				
High N	0.19 ± 0.02	0.18 ± 0.01	8.5 ± 0.4	0.18 ± 0.01
Low N	$0.05 \pm 0.03\,(74)$	$0.08 \pm 0.01\,(56)$	$5.9 \pm 0.5\,(31)$	$0.11 \pm 0.01\,(39)$
Barley				
High N	0.16 ± 0.01	0.16 ± 0.01	7.6 ± 0.4	0.16 ± 0.01
Low N	$0.04 \pm 0.03\,(75)$	$0.12 \pm 0.01\,(25)$	$5.6 \pm 0.2\,(26)$	$0.12 \pm 0.02\,(25)$

Plants were grown in a mixture of peat moss, vermiculite, and sand, and watered with a complete nutrient solution containing either $0.31\,mol\,m^{-3}$ or $5\,mol\,m^{-3}$ NO_3^-. Harvests were made 7 days apart during exponential growth. Leaf areas were measured with an electronic leaf area meter. N content was determined by Conway microdiffusion analysis after micro-Kjeldahl digestion of oven-dried and ground plant material (Radin, Sell & Jordan, 1975). All calculated rates are expressed as mean ± standard error (four trials), with the per cent inhibition by low N in parentheses.

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